In the corner of the eye: camouflaging motion in the peripheral visual field

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Abstract

Most animals need to move, and motion will generally break camouflage. In many instances, most of the visual field of a predator does not fall within a high-resolution area of the retina and so, when an undetected prey moves, that motion will often be in peripheral vision. We investigate how this can be exploited by prey, through different patterns of movement, to reduce the accuracy with which the predator can locate a cryptic prey item when it subsequently orients towards a target. The same logic applies for a prey species trying to localise a predatory threat. Using human participants as surrogate predators, tasked with localising a target on peripherally viewed computer screens, we quantify the effects of movement (duration and speed) and target pattern. We show that, while motion is certainly detrimental to camouflage, should movement be necessary, some behaviours and surface patterns reduce that cost. Our data indicate that the phenotype that minimises localisation accuracy is unpatterned, having the mean luminance of the background, does not utilise a startle display prior to movement, and has short (below saccadic latency), fast movements. [182 words]

Keywords: Motion camouflage; defensive coloration; visual search; peripheral vision; position perception

1. Introduction

If motion breaks camouflage [1, 2], exploring the determinants of detection of a single moving target in central vision can be considered trivial. However, the peripheral visual field is generally a region of diminished resolution [3], so detection of motion need not guarantee successful targeting of a prey that subsequently stops and resumes crypsis. Localisation of a camouflaged target in the periphery is arguably a more ecologically valid characterisation of the early stages of predation than testing detection ability within central vision: there is a low probability that a predator will be looking directly at a concealed prey item at the moment that it starts to move and, by the time attention is focused on the prey, it may have stopped moving and returned to a static camouflaged state. The same holds true for a prey trying to locate a stalking predator.

Previous research on camouflage has focussed predominantly upon the effectiveness of strategies in the absence of motion [4-7], although see [8]. Camouflage operates by exploiting a predator's perceptual system, making detection difficult (*e.g.* by reducing the signal at the stage of lower-level visual processing), and/or manipulating a predator's cognitive mechanisms so that identification is difficult (acting at a higher-level of information processing) [6, 7, 9]. Movement, a salient cue, allows an observer to segregate an object from the background through relative motion information [10, 11]. Movement appears to be incompatible with camouflage, resulting in the general consensus that motion breaks camouflage [1, 2, 8]. However, an organism must often move, whether to get to a point of refuge, a feeding site, or a mating prospect.

Here, using human observers, we investigate a common situation when predators are foraging but have yet to detect a prey item, or a prey item is vigilant in the face of predation risk: the target is most likely to be detected, via its motion, in the predator's peripheral visual field, with attention subsequently brought to bear on it [12]. Localising and responding to a stimulus in the periphery is complicated by the need to take into account cortical transmission and processing delays, as well as those associated with the preparation and

execution of motor actions [13]. Studies on humans suggest that the perceived position of a moving target is predicted via motion extrapolation, and that localisation is affected by the time it takes for the observer to move their eyes toward the target (i.e. the saccadic latency) [13]. Many species use saccades alongside fixations to perceive their environment; typically, these are eye-saccades but can also be head-saccades, in the case of birds, or body-saccades, in the case of insects [14]. Furthermore, many species have a region of the visual field that has a high concentration of cone photoreceptors (*e.g. area centralis*) [see 14, 15; table 3 pg. 187], giving good visual acuity; as eccentricity from this region increases photoreceptor density, and thus acuity, decreases. Amongst other things, the fixate-saccade strategy allows an organism to divert the higher-resolution region of its visual field toward an object [14]. What prey movement strategies might minimise the probability of localisation, and does surface patterning affect this? Here, we focus on two key parameters of transient movement (duration and speed) and their interaction with surface pattern. In addition, we included a flash manipulation, where a highly conspicuous display occurs before target movement. Some, otherwise cryptic, insects reveal conspicuous underwings when they fly. These are usually considered to be displays that startle a predator or interfere with identification [16-19] when the predator has already detected the prey and is initiating an attack. Here, we explore a different possible advantage that occurs when prey movement occurs in peripheral vision: gaze may be 'anchored' upon the initial location by a highly salient but transient display, and subsequent movement masked due to a flash-lag effect [20] or sensory overload [21]. Instead of exploring the effectiveness of motion camouflage strategies with regards to impeding capture, as in motion dazzle experiments [22-28], we aim to explore the phenotype's effects on localisation.

2. Methods

(a) Setup

The control program was written in Matlab (The Mathworks Inc. Natick, MA) with the Psychophysics Toolbox extensions [29-31]. The experiment used two gamma-corrected

21.5” iiyama ProLite B2280HS monitors (Iiyama; Hoofddorp Netherlands), with a refresh rate of 60 Hz, a resolution of 1200 x 1080 pixels, and a mean luminance of 64 cd/m_2, controlled by an iMac (Apple; California, US). The screens were positioned so that the centre of each one was 50 cm from the subject and at an angle of 65° from a fixation cross on a third, not gamma corrected, central screen. At 50 cm each pixel subtended 1.7 arcmin.

During each trial, the participant was shown a square target (48 x 48 pixels), which appeared, moved, and then disappeared. Targets could appear on either the left or right screen (the central screen only displayed the fixation cross). The target moved in a sequence that was dictated by a combination of two movement factors (duration and speed), a pattern factor (see figure 1), and a flash factor (see below for details). Within each trial the target would move on a background generated by a 1/f function [32], representing a generic textured background to which visual systems are hypothesised to be adapted [33]. Spectral analysis of natural scenes shows that amplitude is inversely related to spatial frequency, f; hence the 1/f function [33]. The background was generated afresh every trial. After a random latency (a uniform distribution from 1-3 s, in 0.5 s increments), the target appeared in the centre of one of the two screens at random (probability 0.5), and then moved in a random direction (discrete uniform distribution in the range 1-360°) in a manner determined by the factorial combination of factors described below. The target then disappeared, the non-target screen turned plain grey and the cursor appeared in the centre of the target screen, which retained its 1/f background. In this way, it was unambiguous to the participant on which screen the target had moved; the task was to localise where it had stopped.

Duration of movement (*duration*) had three levels that were designed to bracket saccadic latency for our human observers [34]: 100, 200 & 400 ms. Speed had three levels that were designed to provide a range of velocities (relatively slower and relatively faster) around data on movement speeds of *Zootoca vivipara* [see 35]: 10, 20 and 35 deg/s. A speed of 35, rather than 40 deg/s, was chosen so that targets always remained on the screen. Patterning had three levels (figure 1): black (*Black;* luminance = 0 cd/m_2), grey (*meanLum*; luminance =

64 cd/m2) and background matching (*BG*; *1*/f function, luminance = 66 cd/m2). The background matching function used the same algorithm as that which created the background. Finally, the target could flash briefly prior to movement (maximum luminance = 113cd/m2). This flash factor had three levels: display for 80 ms, 50 ms or not presented at all. The flash was designed to simulate a startle display [16]. It was added prior to movement to explore its putative effect on masking the target's end location.

(b) Task

After the target had finished moving and disappeared, participants clicked a mouse-controlled on-screen cursor (an 8-pixel radius red circle) on the target's estimated final location. The locations of the centre of the target and the cursor were recorded every frame. On each trial, localisation error was computed as the pixel distance between the centre of the target at its final location and the centre of the cursor at the location where it was clicked. The response time for the participant to click the cursor, from the moment at which the target started moving, was also recorded for each trial. Each participant completed six practice trials followed by 162 test trials, which were broken into three blocks of 54. Therefore, participants received all conditions (3 x 3 x 3 x 3) on both screens. Participants were free to take a break between blocks but, in practice, seldom paused for more than a few seconds. The combination of movement and pattern for each trial was independently randomised for every participant. Each trial was completed with the room lights off and with headphones on (to minimise distractions). There were 18 unpaid participants (10 female, ages 18-28), with normal/corrected-to-normal vision, who were naïve to the aims of the experiment. Ethical approval was obtained through the Faculty of Science Research Ethics Committee of the University of Bristol. All participants were briefed and gave their informed written consent, in accordance with the Declaration of Helsinki.

(c) Statistical analyses

Statistical analyses were performed using R (R Foundation for Statistical Computing, www.R-project.org). Both pixel error (*error*) and response time (*RT*) were distributed log-

normally, and so were log10-transformed prior to fitting linear mixed models [function lmer in the lme4 package: 36]. Participant was fitted as a random effect, with fixed effects *speed*, *duration*, *pattern*, *screen* and *flash*. Initially all fixed main effects and their interactions were fitted, followed by backwards stepwise elimination of non-significant terms (based on likelihood ratio tests), starting with the highest order interactions (see electronic Supplementary Material). Within-factor effects were explored using Tukey-type p-values [R package multcomp: 37].

3 Results

Four extremely short response times (under 0.3 s) were outliers (> 5 standard deviations from the mean on the log-transformed scale, when the next lowest was 1.5 standard deviations) and from one participant; these were considered to be premature, accidental, mouse clicks. Five data points were also considered to be response errors because the mouse click was off the target screen (possible, as the mouse could be moved to the central and non-target screens). These nine values comprised only 0.3% of the data and were removed. Localisation error is the primary response variable, but a detailed analysis of response times can be found in the Supplementary Material.

For localisation error, the final model showed significant main effects of the *flash* factor (χ_2 = 7.44, df = 2, p = 0.0242), and screen side (χ_2 = 5.84, df = 1, p = 0.0157), on the participant's localisation accuracy, with no interactions between these and other factors (Fig. 2 and Supplementary Material). Tukey-type pair-wise tests indicated that no flash had a significantly larger error than a flash of 50 ms (z = 2.388, p = 0.0446) and a similar, but non-significant, difference from an 80 ms flash (z = 2.325, p = 0.0523); 50 ms and 80 ms flashes were not significantly different (z = 0.063, p = 0.9978). The effects of the *flash* factor can be seen in figure 2. The main effects of *screen* showed a slightly (2.7%) lower localisation error on the right screen, which suggests a bias that could be attributed to eye preference [38].

Additionally, the model showed that there were significant interactions between the duration of movement and the speed of movement (χ_2 = 11.00, df = 4, p = 0.0266), and the duration of movement and the pattern on the target (χ_2 = 11.24, df = 4, p = 0.0240). To understand these interactions, the data were split by the factor *duration* and the effects of speed and pattern assessed for each level. At the shortest duration, 100 ms, there was no significant effect of pattern (Fig. 2; χ_2 = 1.30, df = 2, p = 0.5219), but at 200 ms there was (χ_2 =10.75, df = 2, p = 0.0046), with mean luminance having the greatest error, significantly greater than black (z = 3.28, p = 0.0030), but not background matching (z = 1.75, p = 0.1872). Black and background matching did not differ (z = 1.52, p = 0.2802). At 400 ms there was also a significant effect of pattern (χ_2 = 19.39, df = 2, p < 0.0001), mean luminance again having the greatest error, significantly greater than black (z = 4.41, p < 0.0001), but not background matching (z = 2.047, p = 0.1013). Background matching also had a greater error than black (z = 2.371, p = 0.0467). Regarding the interaction between duration and speed, at 100 ms there was a significant effect of speed (χ_2 = 22.39, df = 2, p < 0.0001), with a greater error for 35 deg/s than for 10 or 20 deg/s (z = 4.60, p < 0.0001 and z = 3.34, p = 0.0024 respectively); 10 and 20 deg/s did not differ (z = 1.26, p = 0.4155). At 200 ms there was also a significant effect of speed (χ_2 = 34.69, df = 2, p < 0.0001), error increased progressively with speed (Fig.2; 10 vs 20 deg/s: z = 2.47, p = 0.0364; 20 vs 35 deg/s: z = 3.44, p = 0.0017; 10 vs 35 deg/s: z = 5.91, p < 0.0001). At 400 ms there was also a significant effect of speed (χ_2 = 16.93, df = 2, p = 0.0002), with a greater error for 20 and 35 deg/s than for 10 deg/s (z = 3.83, p < 0.0001 and z = 3.25, p = 0.0033 respectively); 20 and 35 deg/s did not differ (z = 0.57, p = 0.8355).

Modelling for response time indicated a significant interaction between pattern and flash when the stimulus moved for 100 ms, with pattern only having a significant effect in the no flash condition (Supplementary Material). Specifically, mean luminance had longer response times than background matching or black patterning, which did not differ. At 200 ms there was a significant effect of flash, with the no flash condition having a longer response time

198 than the flash conditions. At 400 ms there was a significant effect of speed, where an
199 increase in speed increased the response time.

200 **4. Discussion**

201 Unless already detected and fixated, a prey item seeking to avoid a predator, or a predator
202 seeking to approach prey undetected, is likely to be moving within the peripheral visual field.
203 Our data indicate that for such a moving target to minimise its localisation, it should move
204 briefly and quickly, and it should be unpatterned, with similar luminance to the background. A
205 first-order stimulus is defined by intensity differences between target and background, while
206 a second-order stimulus is defined by a difference in some other property, (*e.g.* contrast or
207 pattern). Matching the mean luminance of the target and background pushes the stimulus
208 towards being second-order, and is well known that such stimuli are far weaker than their
209 first-order counterparts [e.g. 39, 40]. A conspicuous flash, such as a startle display, prior to
210 movement does not anchor the predator's saccade to the initial location. In fact, it is
211 detrimental: localisation errors are slightly lower and, for short motion durations, response
212 times considerably shorter, if motion is preceded by a flash. In all treatments, the estimated
213 direction of the target's motion was usually judged fairly accurately, but participants overshot
214 its stopping place (Supplementary Material), for the most difficult targets by more than three
215 body lengths (Figure 2; a 150+ pixel error when the width of the target is 48 pixels). This sort
216 of biased error is frequently observed in motion estimation tasks and is known as
217 representational momentum [13, 41]. In our experiment, greater speed led to greater
218 overshoot, particularly for short duration movements (Fig. 2).

219 Brief movement was the best strategy to increase localisation error, with the greatest errors
220 happening when the duration was shorter than the saccadic latency (100-200 ms) [15, 34,
221 42-45]. Little information is gathered whilst the eyes are saccading [46], and thus stopping
222 before a viewer has had time to complete a saccade and fixate is advantageous.
223 Considering that the fixate-saccade strategy is ubiquitous, this suggests that the prevalence
224 of the intermittent motion observed in many animals [35, 47-54], which is often attributed to

the benefits of image stabilisation for the prey species itself [35, 52, 53, 55], could instead (or additionally) serve to reduce a predator's ability to localise a prey [35, 52]. Avery *et al.* [35] has shown that in the lizard *Zootoca vivipara*, normal movement operates in bursts that broadly correspond to human saccadic latency and, further, a movement speed that approximately corresponds to 20 deg/s. In organisms that are successful at stationary camouflage*,* can change colour [56], or have different appearances through a "flicker-fusion" effect [57], saltatory locomotion could be particularly advantageous. In our experiment, the phenotype that induced the greatest localisation error was plain, with the mean luminance of the background, rather than background-matching in pattern. Cuttlefish that are camouflaged when stationary have been observed to change to a plain colour when moving [56], consistent with what we would predict from our results. Although, for short (100 ms) duration movements, the pattern of the target had no effect on localisation error (Fig. 2), this was at the cost of a far longer response time in the absence of an alerting flash.

Our data show that it is more advantageous to move quickly to reduce localisation accuracy [24]. This seems counter to the typical slow movements used by military operatives [58, 59] and stalking predators [60] and could suggest an alternative; namely, darting between periods of stationary camouflage or refuges/protective cover. There is a significant interaction between the movement duration and the target's movement speed, with increased speed above 20 deg/s having no additional benefit for 400 ms movements. However, this could be an artefact of targets nearing the screen edge in the fast/long-duration combination of treatments, such that the extent of over-estimation was constrained.

A flash before movement does not 'anchor' the viewer's fixation upon the target's starting point. Instead, it appears that the flash cues the viewer to divert their attention towards the target and primes them for the motion that follows, and could hence accelerate the saccade to locate the target in central vision [61]. This contradicts multiple accounts in the literature that deem highly salient patterns as having a startle effect [62-66]; these are proposed to operate by overloading the perceptual mechanisms of the predator with sensory information,

so that a prey animal can escape [21]. However, in the current study the target appears in peripheral vision, away from the focus of attention, and so a startle effect would be unlikely. Also, our results do not support the idea that motion, and subsequent localisation, is masked due to a flash-lag effect. This is likely due to motion continuing beyond the flash-lag processing time and, in order to be effective, flashing should correspond with cessation of movement [17, 18].

The response time data support the conclusions of localisation error, indicating that shorter durations with mean luminance patterning and no flash prior to movement take longer to localise. Target speed had a limited effect on response time when durations were short, but response time increased progressively with target speed when the duration of movement was longer (400 ms), indicating increased uncertainty even when the moving target was in central vision.

Whilst motion is certainly detrimental to camouflage [1, 2] should movement be necessary some behaviours and surface colour patterns reduce that cost [56]. Within the parameters set by our experiment, the phenotype that minimises detection and localisation is unpatterned, has mean background luminance, does not utilise a startle display (no flash) prior to movement, and has short (below saccadic latency), fast movements. It is feasible that predator attention is drawn to the first instance of movement and, subsequently, predators could sit-and-wait for additional movement. However, this presupposes that the predator was able to recognise the source of movement as potential prey, which may not be the case. Additionally, it may not be beneficial for the predator to sit-and-wait for subsequent movement from an uncertain source; continuing to actively search the environment may be more beneficial. Furthermore, we must consider how noisy environments can be (*e.g.* foliage in the wind) and the impact that this may have upon localisation of a moving target [8]. This experiment highlights the importance of addressing ecological problems, whilst also considering the perceptual differences that different regions of the visual field permit. Whilst there are almost certainly quantitative differences across species, the qualitative effects

should remain the same. If we consider the ubiquity of the fixate-saccade strategy [14], and the distribution of photoreceptors that results in a high-resolution region surrounded by an area where resolution drops with increasing eccentricity, we could expect these results to occur in many other species. So, while the speed and mechanism (eye, head or body movement) will no doubt differ between humans and other species, the pattern of results should hold generally. In particular, because limited information is acquired during a viewer's gaze shift, to reduce the probability of being located accurately an animal should move and stop before it can be fixated, and limit the amount of visual information available while moving with colouration that approximates the mean luminance of the background and lacks patterning. It would be very difficult to carry out similar experiments with non-human subjects; we chose humans because it allowed us to be very specific in what we required our observers to do, and what we measured. Our results show that the ability of a (model) predator to localise a target presented in peripheral vision is influenced by different components of movement (duration and speed) and target pattern; motion does not always break camouflage.

Ethics

Participants gave their informed written consent in accordance with the Declaration of Helsinki, and the Ethical Committee of the Faculty of Science, University of Bristol, approved the experiment.

Data accessibility

All data are available from Dryad doi: to be completed upon publication.

Authors' contributions

All authors conceived and designed the experiment; I.E.S. and N.S.S. programmed the experiment; I.E.S. carried out the experiment; I.E.S. and I.C.C. analysed the data; I.E.S. wrote the first draft of the manuscript with subsequent contributions by all authors.

Competing interests

The authors declare no competing interests.

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Figures

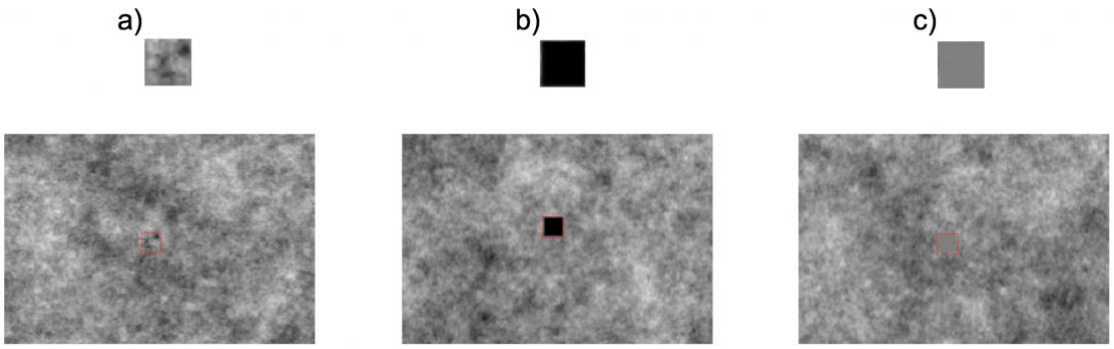

Figure 1 - The target patterning that was used (a) background matching, created using a *1/f* function; (b) black; (c) grey (mean luminance). Below each target is an example of how the target would appear on a background. A red outline has been added to highlight the position of the target on the background (not present during the experiment).

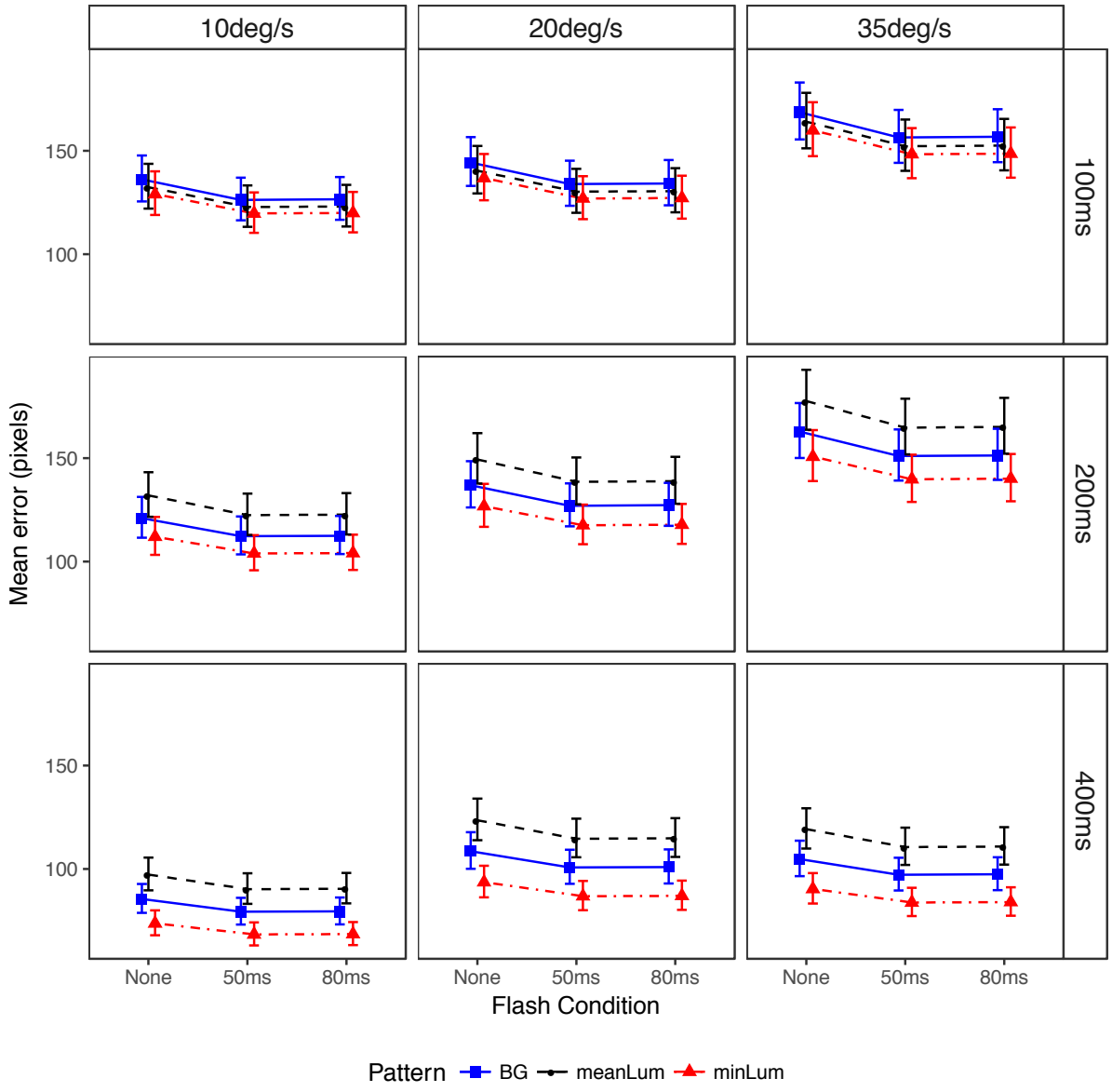

Figure 2 - The mean error associated with the participant's ability to localise a moving object with different movement and patterning conditions, with 95% confidence intervals based on the fitted model (N=18 participants). Different combinations of movement and patterning conditions can be navigated via the panelling. The phenotype with the strongest effect has mean luminance, does not utilise a flash and has short, fast movements. Further, note that the width of the target is 48 pixels, and therefore the aforementioned phenotype is missed by more than three body lengths.

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Table S1. Location error: model simplification steps, starting with a full model (five fixed effects and all possible interactions).

Step	Term removed	χ^2	df	p
1	Flash:Pattern:Screen:Duration:Speed	13.77	16	0.6161
2	Flash:Screen:Duration:Speed	3.36	8	0.9095
3	Flash:Pattern:Duration:Speed	11.05	16	0.8062
4	Flash:Pattern:Screen:Speed	4.59	8	0.8002
5	Flash:Pattern:Speed	1.68	8	0.9894
6	Flash:Pattern:Screen:Duration	7.66	8	0.4672
7	Flash:Screen:Duration	0.12	4	0.9983
8	Flash:Pattern:Screen	1.22	4	0.8749
9	Flash:Pattern:Duration	5.61	8	0.6913
10	Flash:Duration:Speed	9.62	8	0.2931
11	Flash:Duration	1.24	4	0.8723
12	Flash:Pattern	5.40	4	0.2484
13	Flash:Screen:Speed	6.30	4	0.1780
14	Flash:Screen	0.28	2	0.8697
15	Flash:Speed	2.63	4	0.6222
16	Pattern:Screen:Duration:Speed	11.53	8	0.1737
17	Pattern:Screen:Duration	0.89	4	0.9259
18	Pattern:Duration:Speed	5.16	8	0.7401
19	Screen:Duration:Speed	4.24	4	0.3746
20	Screen:Duration	1.33	2	0.5134
21	Pattern:Screen:Speed	8.85	4	0.0650
22	Screen:Speed	0.33	2	0.8489
23	Pattern:Screen	1.11	2	0.5741
24	Pattern:Speed	7.45	4	0.1139

The initial (saturated) model was ~ Flash*Pattern*Screen*Duration*Speed + (1 | Subject). Significance was assessed using likelihood ratio tests.

Analysis of response time

The final model contained a significant two-way interaction between duration and speed (χ^2 = 29.88, df = 4, p < 0.0001), and a three-way interaction between duration, pattern and the flash prior to the target moving ((χ^2 = 21.74, df = 8, p = 0.0054) (Fig. S1; Table S2). To explore the nature of these interactions the data were split by duration, and models fitted with speed, pattern, flash and the two-way interaction between the latter two factors. For 100 ms movements, speed was not significant (χ^2 = 0.67, df = 2, p = 0.7150), but the pattern x flash interaction was (χ^2 = 26.14, df = 4, p < 0.0001). Analysing the flash conditions separately, with no flash, pattern was significant (χ^2 = 26.29, df = 2, p < 0.0001), with the mean luminance pattern having longer response times than black (z = 4.70, p < 0.0001) and background matching (z = 4.32, p < 0.0001), with the latter two treatments not differing (z = 0.40, p = 0.9170). However, when movement was preceded by a flash, there was no significant effect of pattern (50 ms: χ^2 = 2.75, df = 2, p = 0.2530; 80 ms: χ^2 = 0.16075, p = 0.9228).

For 200 ms movements, the pattern:flash interaction was not significant (χ^2 = 3.33, df = 4, p = 0.5039). So, removing this term and simplifying the model sequentially, neither pattern (χ^2 = 4.79, df = 2, p = 0.0914) or speed (χ^2 = 5.58, df = 2, p = 0.0613) were significant, but flash was (χ^2 = 35.03, df = 2, p < 0.0001), with response times longer for no flash than when a flash preceded movement (no flash vs 50 ms flash: z = 4.28, p < 0.0001; no flash vs 80 ms flash: z = 5.74, p < 0.0001; 50 ms vs 80 ms flash: z = 1.46, p = 0.3080).

For 400 ms movements, the pattern x flash interaction was not significant (χ^2 = 4.10, df = 4, p = 0.3927). So, removing this term and simplifying the model sequentially, neither pattern (χ^2 = 0.48, df = 2, p = 0.7865) or flash (χ^2 = 4.95, df = 2, p = 0. 0841) were significant, but speed was (χ^2 = 70.92, df = 2, p < 0.0001), with response times increasing with target speed (10 vs 20 deg/s: z = 3.565, p = 0.0011; 10 vs 35: z = 8.53, p < 0.0001; 20 vs 35: z = 4.98, p < 0.0001).

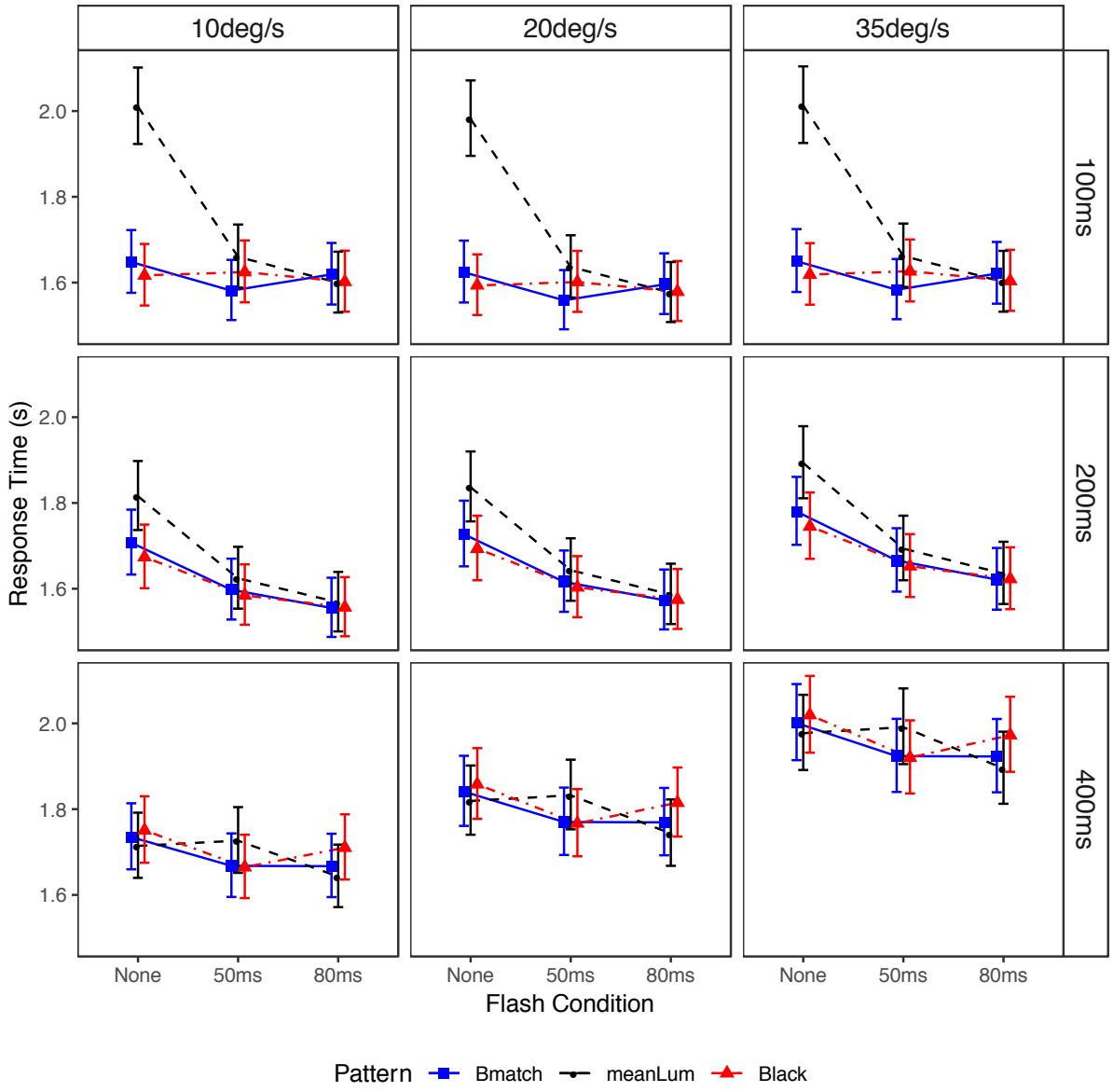

Figure S1 - The response time for participants trying to localise a moving object with different movement and patterning conditions, with 95% confidence intervals based on the fitted model (N=18 participants). Different combinations of movement and patterning conditions can be navigated via the panelling. The phenotype with the strongest effect has mean luminance, does not utilise a flash and has short and/or fast movements.

Table S2. Response time: model simplification steps, starting with a full model (five fixed effects and all possible interactions).

Step	Term removed	χ^2	df	p
1	Flash:Pattern:Screen:Duration:Speed	16.29	16	0.4333
2	Flash:Screen:Duration:Speed	2.26	8	0.9720
3	Pattern:Screen:Duration:dotShift	5.67	8	0.6846
4	Pattern:Screen:Duration	1.22	4	0.8746
5	Flash:Pattern:Duration:dotShift	13.46	8	0.6389
6	Pattern:Duration:dotShift	4.27	8	0.8321
7	Flash:Screen:Duration:dotShift	9.86	8	0.2749
8	Flash:Screen:Duration	1.21	4	0.8756
9	Screen:Duration:dotShift	3.27	8	0.5130
10	Screen:Duration	0.35	2	0.8375
11	Flash:Duration:dotShif	11.36	4	0.1821
12	Flash:Pattern:Screen:dotShift	13.94	4	0.0835
13	Flash:Pattern:Screen	2.95	4	0.5655
14	Flash:Pattern:dotShift	9.11	8	0.3331
15	Pattern:Screen:dotShift	5.75	4	0.2187
16	Pattern:Screen	1.32	2	0.5165
17	Pattern:dotShift	7.67	4	0.1046
18	Flash:Screen:dotShift	8.04	4	0.0902
19	Flash:Screen	0.21	2	0.9018
20	Screen:dotShift	3.51	2	0.1725
21	Screen	0.03	1	0.8599
22	Flash:dotShift	7.55	4	0.1096

The initial (saturated) model was ~ Flash*Pattern*Screen*Duration*Speed + (1 | Subject). Significance was assessed using likelihood ratio tests.

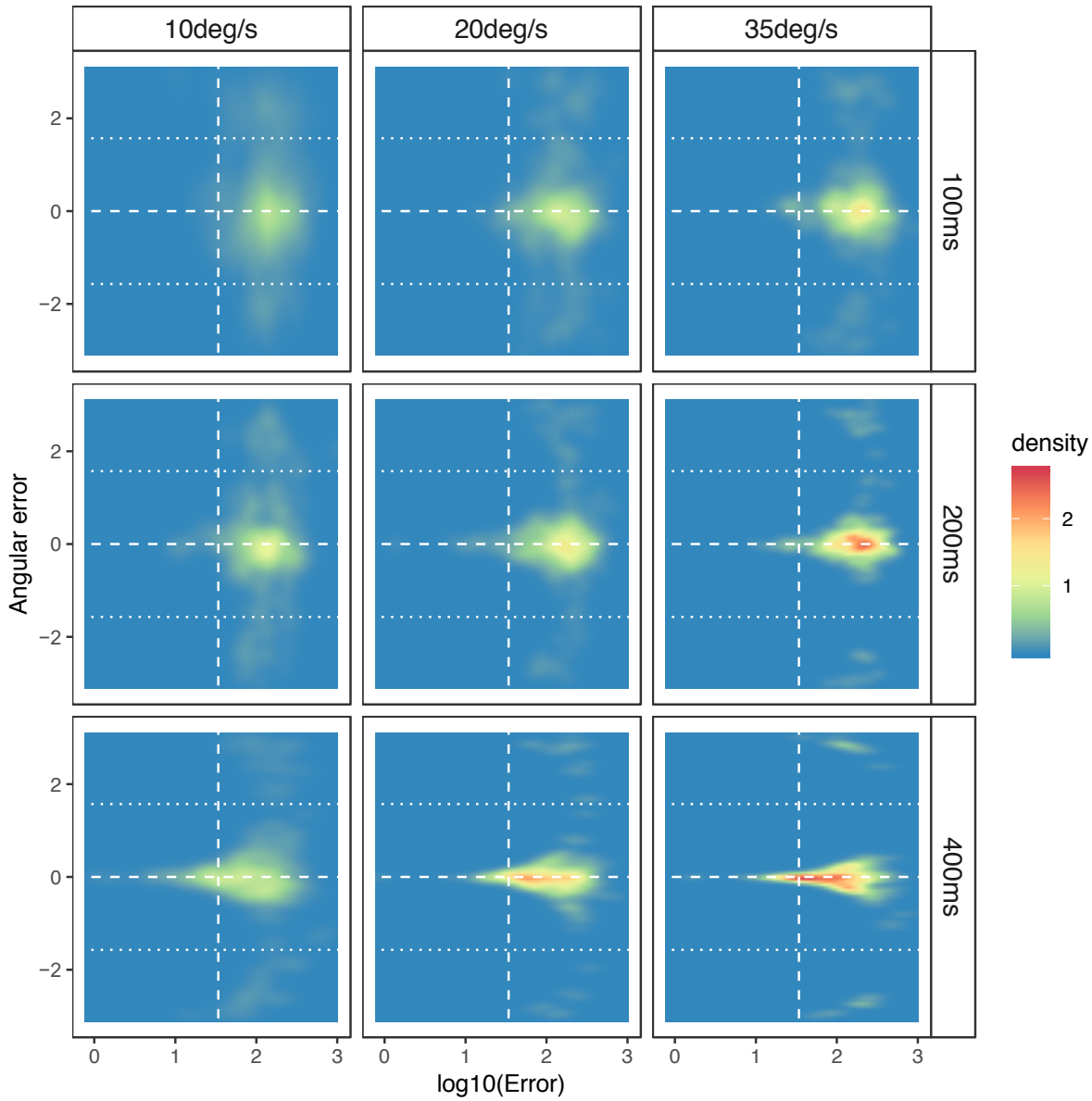

Figure S2 – Angular error (relative to the target's trajectory) plotted against the log-transformed localisation error (distance from target) in pixels for participants trying to localise a moving object with different movement and patterning conditions (N=18 participants). Different combinations of movement and patterning conditions can be navigated via the panelling.